Fossil Mammals of Africa
No. 17

FOSSIL METACARPALS FROM SWARTKRANS

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With 2 plates and 2 figures in the text

FOSSIL MAMMALS OF AFRICA

INTRODUCTION

In a brief communication, Broom & Robinson (1949a) reported the recovery of a 1st metacarpal bone from Swartkrans; subsequently these authors attributed this bone to *Paranthropus*. A further metacarpal fragment was later recovered from the Swartkrans site but from a lower level in the deposit. No account of this second fragment has so far been published. The recent discovery of stone artefacts (Robinson & Mason, 1957) in the red-brown breccia of the Sterkfontein Extension Site makes a further study of the thumb metacarpal (S K.84) and a description of the other metacarpal (S K.85) of particular interest. Special attention has therefore been given to the possible function of the thumb in relation to prehensility.

DESCRIPTION OF MATERIAL

Metacarpal fragment S K.85. (4th L.)

The specimen is well preserved and consists of the distal half of an adult metacarpal bone (Pl. 1, figs. 5–8; Text-fig. 1). The bone has a rectangular-shaped distal articular surface which is curved in both antero-posterior and lateral planes. The head is asymmetrical in relation to the shaft, being slightly flattened on its left side (Pl. 1, fig. 5). The shaft is curved longitudinally, and from the front is asymmetrical, being more curved on the right than on the left side. The central beak and sesamoid impressions, so prominent a feature of S K.84, are minimal. Muscular ridges demarcating the dorsal extent of the insertion of the interosseus muscles are well marked, giving the shaft a somewhat compressed appearance from side-to-side. These ridges meet in a distinct dorsal interosseus crest towards the proximal end of the fragment (Pl. 1, fig. 7).

The dimensions of the fossil bone are:

Overall length of fragment	32·5 mm.
Transverse width at narrowest part of shaft . . .	6·5
Antero-posterior width at narrowest part of shaft . .	8·0
Transverse width of distal articular surface . . .	8·0
Antero-posterior width of distal articular surface . .	11·0

This bone is provisionally identified as the 4th metacarpal for the following reasons:

1. Asymmetry of the metacarpal head is minimal. Marked asymmetry is found in Man in both 2nd and 5th metacarpals. On this criterion alone the fragment can be attributed to either 3rd or 4th digit.
2. The shaft is asymmetrical. In both Man and Ponginae the 3rd metacarpal shows a similar curvature on both medial and lateral sides, whereas the 4th metacarpal shaft is frequently asymmetrical.

The asymmetry of the head results in a slight flattening of the distal articular surface that, together with the increased curvature on the contralateral side of the shaft, suggests that the fossil bone is of the left hand.
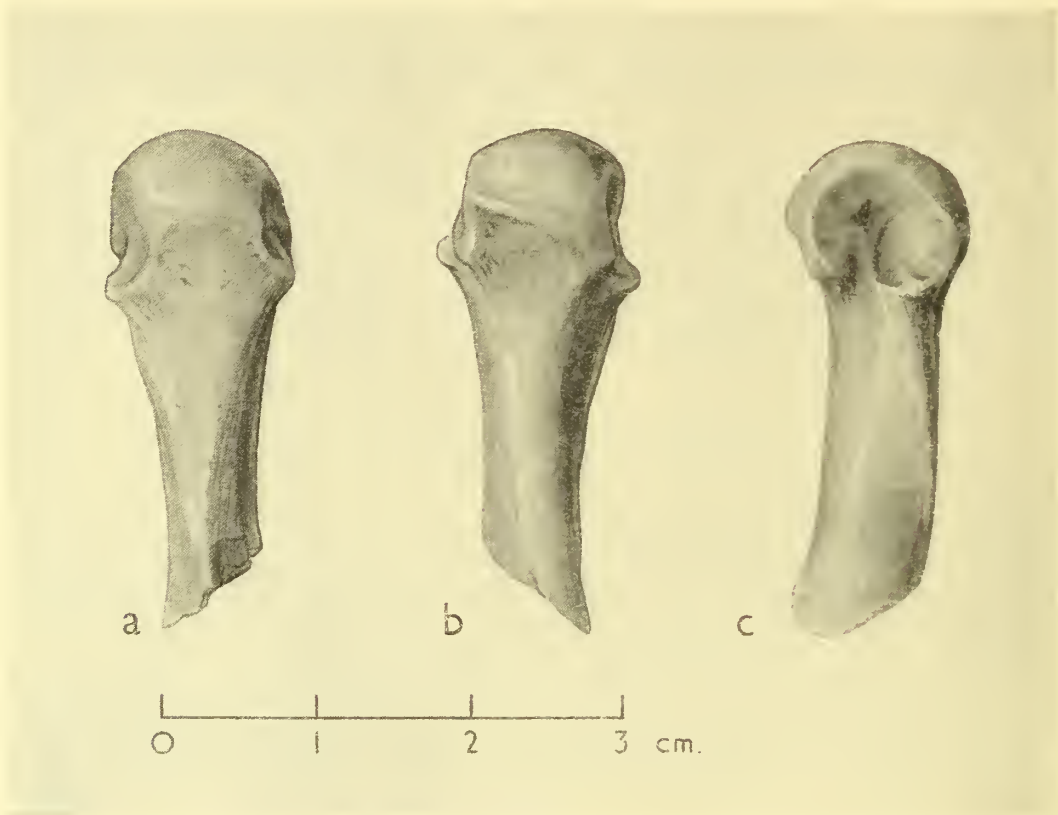
FIG. 1. S K.85   Three views of the 4th metacarpal fragment (L).   (*a*) posterior aspect; (*b*) anterior aspect; (*c*) right lateral aspect.   × 2.

COMPARATIVE OBSERVATIONS

The fossil fragment was compared with adult human and anthropoid ape 4th metacarpals.   The general appearance is very similar to that of modern European Man, differing only in the absence of the buttress of bone that sweeps down to the anterior edge of the articular surface.   This buttress is apparent in the profile view of some, but not all, human metacarpals (Pl. 1, figs. 2, 4).   A dorsal interosseus crest occurs in over half of the human 4th metacarpal series (24 in a total of 41) and interosseus ridges are apparent in all.   In none of the human bones, however, is the crest as sharply defined as it is in the fossil form.

The 4th metacarpal fragment is distinguished from the same bone of anthropoid apes in the following particulars:

1. In chimpanzee, orang and gorilla, the head of the metacarpal is set at an angle to the shaft, the articular surface being directed anteriorly as well as distally (Pl. 1, figs. 9–12). In the fossil bone the head is set in the line of the shaft and the articular surface points distally (Pl. 1, fig. 6).
2. In gorilla, chimpanzee and sometimes the orang there is a distinct articular shelf where the posterior edge of the articular surface meets the shaft (Pl. 1, figs. 10, 12). This shelf is absent in the fossil form.
3. The dorsal interosseus ridges and crest are absent or poorly developed in chimpanzee and absent in orang and gorilla (Pl. 1, fig. 11). The ridges and crest are well marked in the fossil bone.

The fossil fragment is curved laterally in its longitudinal axis. The shaft of the 4th metacarpal is habitually curved in Man; among the Ponginae a curvature is usually present in the gorilla (Pl. 1, figs. 10, 12), well marked in the chimpanzee but frequently absent in the orang.

LENGTH RECONSTRUCTION.—The original length of the fossil fragment has been estimated by means of the index:

$$\frac{A.P.\ \text{diameter of head} \times 100}{\text{length}}$$

In modern European Man this index is fairly constant for the 4th metacarpal, having a mean value of 21·7 ($S.D. = 1·6$) in a small series of 41 bones from separate individuals. Application of the mean figure to the fossil specimen gave it a calculated length of 50·7 mm. The lower and upper standard deviation range provides calculated lengths of 54·7 mm. and 47·2 mm. respectively. On the basis of this index the fossil 4th metacarpal appears to be markedly shorter than an average human bone where a mean overall length of 56·0 mm ($S.D. = 3·3$) is found.* From these figures it is inferred that the fossil bone was considerably shorter than the average human bone but that nevertheless its length lies within range for modern European Man.

In summary the 4th metacarpal fragment shows the following hominid features:

(a) The distal articular surface is rectangular in shape.
(b) Grooves for sesamoid bones are absent.
(c) The head of the bone is aligned with the shaft.
(d) A posterior articular shelf is absent.
(e) The posterior attachments for the dorsal interosseus muscles extend on to the posterior surface of the shaft and leave strong impressions that meet in a dorsal ridge.

* In a series of 100 radiographs of the human hand (author's collection) the mean length of the 4th metacarpal was as follows:

Adult males   (50) 59·9 mm. ($S.D.$ 3·9)
Adult females (50) 55·3 mm. ($S.D.$ 3·5)

Metacarpal S K.84.   (*1st L*)

The specimen is perfectly preserved and is complete apart from a slight irregularity of the shaft at about its mid-point.   X-ray examination of the fossil bone reveals that underlying the surface irregularity there is a transverse fracture that presumably occurred during fossilisation.   The fracture has resulted in some forward angulation of the distal fragment which has had the effect of exaggerating the longitudinal curvature of the shaft.   The fossil bone is an adult specimen and is short and robust and quite strongly curved in its longitudinal axis; the shaft is triangular in cross-section and bears strong muscular markings on both medial and lateral aspects (Pl. 2, figs. 17–20; Text-fig. 2).   At the proximal end there is a well-developed, saddle-shaped articular surface.   The distal articular surface is asymmetrical, being flattened on its lateral aspect; the articular surface narrows from front to back, so that its appearance is somewhat heart-shaped.

FIG. 2. S K.84.   Two views of the 1st metacarpal (L).   (*a*) anterior aspect; (*b*) left lateral aspect.   × 2.
A cast of this specimen is in the possession of the British Museum (Natural History).   Catalogue Number E M.152.
(Drawings by Audrey Besterman.)

There is a prominent beak projecting forwards from the anterior edge of the articular surface; this beak is flanked on either side by short, shallow grooves presumably related to sesamoid bones; the medial groove is deeper than the lateral one.

The dimensions of the fossil bone are:

Maximum length	35·0 mm.
Antero-posterior width in mid-shaft . .	7·5
Transverse width in mid-shaft . . .	9·5
Maximum transverse width at base . .	12·5
Maximum transverse width at head . .	11·0

Method of study

The fossil bones have been studied by comparing them with those of Recent Man and certain of the modern Pongidae.

The material used in this investigation consisted of adults of the following genera:

Pan . .	13 individuals	
Pongo . .	10	
Gorilla . .	16	
Homo . .	177	(including 19 Bushman)

The source, sex and history of the pongid and Bushman material is summarised in the Appendix. The remaining human material was derived from collections held by several Departments of Anatomy in London; unfortunately the race of these bones is unknown but is presumed to be predominantly European and is referred to below as European Man.

The following measurements were made on both the fossil and Recent material:

1. *Maximum length* of the 1st metacarpal bone in line with the longitudinal axis.
2. *Antero-posterior width* of 1st metacarpal in mid-shaft region.
3. *Lateral width* of 1st metacarpal in mid-shaft region.

The results of the measurements for the fossil bone and for Ponginae are fully set out in the Appendix.

COMPARATIVE OBSERVATIONS

The fossil 1st metacarpal bone was compared with that of European Man and certain modern Pongidae with particular reference to: (*a*) absolute length of the thumb; (*b*) prehensile power of the thumb; (*c*) mobility of the thumb.

Absolute length of the thumb

The lengths of the 1st metacarpals in the comparative series are summarised in Table I (see also Appendix).

It will be seen from this table that the fossil bone corresponds in length with the shortest chimpanzee 1st metacarpal, but falls outside the range for European Man, gorilla and orang and just within the Bushman range. The figures for the standard deviation suggest that there is probably a significant difference between the length of the fossil bone and that of European Man, the gorilla and the orang. Further evidence of the human length range is provided by a series of unpublished measurements made by the late Professor A. Macalister of Cambridge University on 180

adult human 1st metacarpal bones.   The shortest metacarpal in his series measured 37 mm., a figure that corresponds closely with the length of the shortest metacarpal found in the present series.

TABLE I

	Number	Range (mm.)	Mean length (mm.)	Standard deviation
European Man . .	166	37·3–53·0	44·6	3·1
Bushman . .	19	34·5–48·9	40·0	4·3
Chimpanzee . .	13	35·0–48·5	38·6	4·5
Gorilla . . .	16	39·0–55·5	46·0	4·8
Orang-utan . .	10	45·5–56·5	50·8	4·2
Fossil bone (S K.84) .	1	—	35·0	—

Prehensile power of the thumb

(*a*) ROBUSTNESS.—The robustness of the bone has been assessed by calculating the mean of two diameters at right angles at mid-shaft, and expressing it as a proportion of the total length thus:

$$\frac{\text{Mean diameter mid-shaft} \times 100}{\text{length}}$$

The results of these measurements are summarised in Table II.

TABLE II

	Number	Range (mm.)	Mean index (mm.)	Standard deviation
European Man . .	166	18·9–27·3	23·0	1·9
Bushman . .	17	15·1–25·5	21·6	2·5
Gorilla . . .	13	18·3–26·1	20·6	2·2
Orang-utan . .	10	13·2–19·0	16·2	2·0
Chimpanzee . .	16	16·5–22·2	19·1	2·2
Fossil bone (S K.84) .	1	—	24·3	—

It is apparent that while the index of robustness of the fossil bone is above the mean index for European Man, and well above that for the anthropoid apes, the index falls within the gorilloid and also within the range for European Man and for Bushman. When the relative shortness of the fossil bone compared with European Man and gorilla (Table I) is taken into account its relative stoutness is more apparent.

(*b*) MUSCULARITY.—The muscle attachments on the fossil bone are strongly marked, particularly on the radial margin where there is a prominent ridge for opponens pollicis along the whole length of the lateral margin of the shaft; the distal half of this ridge is irregular.   This irregularity is usually well marked in Man (Pl. 2,

fig. 14), gorilla (Pl. 2, fig. 22) and some chimpanzees, but poorly marked in the orang and in lower catarrhines. The medial aspect of the shaft is also strongly moulded in its proximal half at the site of origin of the 1st palmar interosseus, and is rough and irregular in its distal half in the region where the 1st dorsal interosseus is attached. Strong moulding in the proximal half is commonly found in Man but not in the anthropoid apes; whereas the roughening of the distal half is common in the apes but is not particularly so in Man.

(c). The longitudinal curvature of the shaft is a striking feature of the fossil bone—even after due allowance has been made for angulation following the post-mortem fracture. This curvature is in contrast to the human pattern, where the 1st metacarpal is invariably straight (Pl. 2, figs. 14, 16); the thumb metacarpal of the gorilla (Pl. 2, figs. 22, 24) and the chimpanzee (Pl. 2, figs. 26, 28) is either straight or very slightly curved, while the curvature of the orang bone is usually well marked (Pl. 2, figs. 30, 32).

(d) SESAMOIDS.—The central beak projecting from the anterior edge of the articular surface of the fossil bone flanked by short grooves at either side strongly suggest the presence of paired sesamoid bones. A beak of this size and prominence has not been observed in any individual of the human or anthropoid ape series; a small protuberance is occasionally seen on the human 1st metacarpal, as Broom & Robinson (1949) pointed out, but it never reaches the prominence of that shown by the fossil bone. No central protuberance of this nature was observed in the anthropoid ape series.

The size of the groove on the medial side of the fossil bone indicates that the medial sesamoid was somewhat larger than the lateral. Predominance of the medial sesamoid is a condition frequently found in Man.

Mobility of the thumb

The assessment of mobility is based on the form of the base and the head of the 1st metacarpal.

(a) BASE OF 1ST METACARPAL.—At the proximal end of the bone there is a well-marked, saddle-shaped articular surface particularly strongly curved in the medio-lateral plane indicating a good range of abduction and adduction.

This joint is extremely variable in Man as it is in anthropoid apes, and particularly in the chimpanzee (Mivart, 1867); individual bones vary greatly in the length and depth of their articular curvatures. In the orang the antero-posterior concavity is invariably poorly marked, while the lateral convexity is usually well developed (Pl. 2, figs. 29–32). In the gorilla the antero-posterior concavity is invariably long and deep and the lateral convexity constitutes a long segment extending well on to the lateral and medial aspects of the bone (Pl. 2, figs. 21–24). In Man the antero-posterior concavity is usually better developed than in the orang but is shorter and shallower than in the gorilla, the medio-lateral convexity extending less far on to the medial side of the bone (Pl. 2, figs. 13–16). The fossil bone has an antero-posterior curvature similar in depth and length to that found in Man, but it resembles the gorilla and the degree to which the articular surface extends on to the medial aspect of the shaft (Pl. 2, figs. 17–20).

2—(170)

(b) HEAD OF 1ST METACARPAL.—The head of the fossil bone is strongly curved in a lateral plane constituting the arc of a circle of 6 mm. radius. Estimates of curvature were made by matching with curves of known radius etched on Perspex.

In the human series all specimens showing any degree of arthritic change were excluded. Evidence of this disease was seen in 46 out of 134 specimens. No instances of osteo-arthritic change were found in the gorilla or orang series, but among the chimpanzee metacarpals four specimens were found to be affected.

In Table III the curvature of the Bushman metacarpals are included in the human series and the anthropoid apes are grouped together:

TABLE III

	Number of specimens	Radius of curvature less than 10 mm.	Radius of curvature between 10–30 mm.	Radius of curvature greater than 30 mm.	Range
Human (including Bushman) . .	99	5	87	8	8–100
Anthropoid ape . .	36	23	13	0	4–20

While the method for estimating curvature is reasonably accurate, the figures show such wide variation that they do not merit statistical treatment. It is apparent that the curvature of 6 mm. for the head of the fossil bone is, however, outside the human range in this series and within the range for anthropoid apes.

The articular surface of the fossil bone narrows from front to back, and in this respect is quite unlike the human metacarpal, in which the surface is invariably rectangular, as it is in the chimpanzee. Orang and gorilla have a somewhat heart-shaped surface as do the lower catarrhines.

(c) OBLIQUITY OF DISTAL ARTICULAR SURFACE.—A lateral obliquity of distal articular surface, giving the appearance of a tilted head, is habitually found in the gorilla, the orang-utan and the chimpanzee; it is most marked in the orang and the least marked in the chimpanzee (Pl. 2, figs. 21, 25, 29). Lateral obliquity is occasionally found in Man but is never as marked as that seen in the orang and the gorilla. The fossil bone shows a moderate degree of obliquity of the articular surface (Pl. 2, fig. 17) towards the lateral side.

The comparative findings indicate that the fossil metacarpal is of a general hominoid type. The only features in which it shows a resemblance to Man relate to its robustness and muscular attachments. In several particulars the fossil bone bears a strong similarity to the anthropoid apes:

1. The longitudinal curvature of the shaft.
2. The lateral elongation of the saddle surface.
3. The shape, curvature and obliquity of the articular head.

The length of the bone is outside the range for gorilla, orang and modern European Man, but within the range for Bushman and chimpanzee. The prominent beak

between the sesamoid facets on the head of the bone has not been observed in any specimen—human or pongine—in this series although an incipient beak is occasionally seen in Man. This process appears to be unique in this particular situation and, while it can be regarded as an aberrant feature of considerable functional significance, it is presumed to be of no particular taxonomic value.

FUNCTIONAL CONSIDERATIONS

THE 4TH METACARPAL.—The shape of the distal articular surface and its alignment relative to the shaft indicates a full range of abduction and adduction and minimal hyperextension. The articular shelf seen on the posterior aspect of the metacarpal heads in chimpanzee and gorilla is absent. This shelf is presumably related in the Ponginae to the hyperextension of the digits during quadrupedal walking when the weight of the upper trunk is borne on the dorsum of the middle phalanges. In this respect it is interesting to note that the articular shelf is most prominent in the most terrestrial of the three genera and least well marked in the most arboreal.

The strong interosseus markings of the fossil bone suggest the presence of powerful muscles and therefore of divergent metacarpals and of a broad span to the hand.*

THE 1ST METACARPAL.—The extreme shortness of the thumb metacarpal which falls just within the range for the Bushman series but well outside the range for the modern European Man series may simply be a reflection of stature.

The observation that the length of the fossil metacarpal corresponds approximately to the shortest metacarpal in the Bushman series suggests a stature corresponding to the low average height of Bushman. According to Wilder (1926) and Bean (1931) this figure would be above 4 ft. 8 in. Robinson (1958, personal communication) estimates the height of *Paranthropus* to be between 5 and 6 ft., but not exceeding the latter. He points out that this estimate is necessarily of a provisional nature, the only evidence of stature available being an innominate bone that roughly corresponds in height to that of a large Bantu male. Thus, if Robinson's estimate of height of *Paranthropus* is anywhere near the correct figure, the Swartkrans thumb metacarpal would appear to be too short for this form. On the other hand to exclude *Paranthropus* on the basis of a metacarpal size is to assume that limb length indices of modern man are relevant in the case of *Paranthropus*. There is, therefore, still the possibility that the shortness of the metacarpal is a reflection not of stature but of a short hand or of a short thumb. The observations made below with regard to the obliquity of the distal articular surface suggest that the latter alternative is the more probable, and that the fossil bone belonged to a thumb that was disproportionately short compared to the rest of the hand.

The fossil 1st metacarpal is clearly more robust than is general in anthropoid apes and European Man, irrespective of absolute length differences. When the length of the fossil bone is taken into consideration and compared with those forms with which

* The orang-utan when on the ground frequently bears weight on the dorsum of the *proximal phalanges* rather than on the *middle phalanges*. This behavioural characteristic may account for the rarity of the articular shelf in these forms.

it is most nearly comparable, e.g. chimpanzee and Bushman, it is apparent that it is considerably more robust than all Bushman and chimpanzee bones (Pl. 2, figs. 25–28) examined.

The extent and degree of muscular markings not only correlates with the robusticity of the bones but also suggests a closer affinity with the human pattern of muscular activity than with that of the anthropoid apes.

The curious beak on the metacarpal head which is presumed to indicate the presence of large sesamoids is an aberrant feature and is found in neither the pongine nor the human series.   The homologue of this structure is seen under the head of the 1st metatarsal in Man where the large weight-bearing sesamoids are sited in gutters on either side of a central crest.   The absence in the fossil bone of any grooves extending on to the articular surface confirms that the fossil hand was in no way weight-bearing; deep grooves in this situation are found in the human hallux and, associated with a central crest, on the weight-bearing metacarpal heads of quadrupedal monkeys.

In general it would appear that the stoutness, the muscularity and the large sesamoid element, particularly the medial sesamoid which receives the insertion of adductor pollicis, indicate a thumb of prehensile power equal or in excess of that found in modern gorillas and modern Man.

Evidence regarding the mobility of the thumb is provided by the saddle-surface which is particularly well developed in the abduction-adduction plane and also by the shape of the distal articular surface.

The lateral obliquity of the distal articular surface of the fossil bone would appear to indicate that active abduction was habitually carried out at this joint, as it is in the Ponginae.   A similar obliquity is seen on the head of the 5th metacarpal in Man, where it is clearly related to the wide range of abduction of the little finger.

The significance of an increased abduction range at the metacarpo-phalangeal joint in the Ponginae may be related to the specialised brachiating mode of locomotion of these forms.   In the specialised pongid brachiators there is a disproportion between the length of the thumb and that of the remaining digits.   It is this relative shortness of the thumb that makes it impossible for the chimpanzee, orang or gibbon to adopt the posture of thumb-index finger opposition that is the basis of precision movements of the hand in Man (Napier, 1956).   The shortness of the thumb of brachiators may be correlated with the length of their fingers, for the effectiveness of specialised brachiation depends on the unimpeded grasp of the hooked fingers on overhead handholds; a thumb elongated in proportion to the length of the fingers would only hinder this action.

A thumb capable of being abducted widely in a plane at right angles to the palm would appear to be part of the same adaptation.   In gibbons, a wide range of abduction takes place at the carpo-metacarpal joint, which is of "ball-and-socket" variety, while the first interdigital space is deeply cleft to facilitate the movement. In orang-utan, gorilla and chimpanzee the increased abduction occurs mainly at the metacarpo-phalangeal joint where, as already noted, the articular surface is set obliquely to the shaft; in the same genera the width from side to side of the proximal metacarpal articulation indicates that a considerable range of abduction is also possible at the carpo-metacarpal joint.

The obliquity of the distal articular surface of the fossil bone and the evidence provided by the carpo-metacarpal joint of a wide range of abduction and adduction may be interpreted as not only indicating a high degree of mobility but also the presence of some disproportion between the length of the thumb and the length of the fingers.

GENERAL CONCLUSIONS

The fossil metacarpals were recovered from the same site and at the same level as the remains of the *Paranthropus* and *Telanthropus* (Broom & Robinson, 1949, 1950; Robinson, 1953, 1954). As no other australopithecines have been found at Swartkrans it may be assumed for the present that the fossil bones belong to one or other of these forms. The two fossil metacarpals, however, were not associated in the Swartkrans deposits, the 4th metacarpal belonging to a slightly earlier horizon. There is, therefore, no particular reason for believing that the fossil bones pertain to the same species or even the same sub-family. In fact, apart from a general correspondence in size and texture, the two bones have little in common. The thumb metacarpal has rather more affinities with the Ponginae than with the Homininae, while the 4th metacarpal—except in the matter of size—fits essentially into the pattern seen in modern Man. The robustness of the 1st metacarpal and the aberrant nature of the beak-like process incline one to associate this bone with *Paranthropus*, which is known to be an extremely robust form and somewhat aberrant in its known morphology. The 4th metacarpal fragment on the other hand is not excessively robust and lacks the specialised features associated with pongid metacarpals. In the absence of these pongid characters and in the possession of strong interosseus markings terminating in a well-defined crest, the fossil fragment shows marked affinities with modern Man. The striking differential affinities between the thumb metacarpal and the 4th metacarpal fragment make it highly unlikely that both could have come from the same species. It is assumed therefore that the 4th metacarpal does not pertain to *Paranthropus*. The only other hominid so far recovered from Swartkrans site is *Telanthropus*, a form regarded by Robinson as being transitional between the prehominid and euhominid grades and placed by him (1953) in a separate sub-family, the Euhomininae. Le Gros Clark (1955) has expressed the doubts held by several students regarding the validity of giving *Telanthropus* a sub-family or even generic distinction; Robinson's view, however, has received recent support from Wells (1958). Whatever the precise systematic status of *Telanthropus*, the fact remains that a form more advanced along the human line than *Australopithecus*, and less aberrant and less robust than *Paranthropus*, is represented in the Swartkrans breccias. It is concluded therefore that the 4th metacarpal fragment belongs either to a hominid as yet unknown at Swartkrans or to *Telanthropus* itself.

The robustness, the muscular markings, the mobility of the proximal and distal articulations of the 1st metacarpal and the indications of large sesamoids (particularly on the medial side where the sesamoid is related to the insertion of adductor pollicis), all suggest that the hand was not only capable of prehension but possessed an extremely powerful grip.

There is now undisputed evidence of a lithic industry in association with the remains of *Australopithecus* (Robinson & Mason, 1957). The stone tools found at Sterkfontein indicate a culture showing marked similarities to Chelles-Acheul stage of the African Stone Age Sequence. The presence of stalagmite overlying the tool-bearing breccia indicates that the site was originally a cave, and this, together with the two milk molars attributed to *Australopithecus* found in association with the artefacts in the floor deposits, strongly suggest that the cave was at one time used as a dwelling place, though not necessarily by *Australopithecus*.

Robinson (1956) and Robinson & Mason (1957) attributed the lithic culture at Sterkfontein to *Telanthropus* and not to *Australopithecus*, mainly on the grounds that the culture was too advanced for a form with the brain size of *Australopithecus*. Robinson suggests that it was likely that the tools were the work of a more progressive hominid such as he believes *Telanthropus* to have been. Robinson also points out that the form with the most advanced morphological features in the known material from the Sterkfontein Valley, and at the relevant time level, is *Telanthropus*, and that therefore to attribute the most advanced activity to the creature with the most progressive morphology is the logical step. Oakley (1951) at one time considered it unlikely that *Australopithecus* was a tool maker on the grounds of brain size, but in the light of the new evidence from Sterkfontein he has revised his opinion (1957). Oakley, however, hesitated to accept *Telanthropus* as the maker of the Sterkfontein tools in view of the fact that the Swartkrans breccia is on a later time horizon than the Sterkfontein tool-bearing layer. As Swartkrans follows Sterkfontein in the local geological sequence, and as Sterkfontein is now believed to contain something higher than was originally thought, it seems possible that the lower levels of the Swartkrans breccias overlap the upper levels of Sterkfontein. *Telanthropus* remains have been found in the lower levels at Swartkrans, so that the temporal discrepancy may, in fact, turn out to be insignificant. The geographical proximity of the two sites, which lie less than a mile apart, provides additional, though circumstantial, support for Robinson's view.

The present absence of artefacts of any sort at Swartkrans* in association with *Telanthropus* and the absence of any remains of this form in the Sterkfontein tool-bearing breccias provide further grounds for scepticism. It is possible, however, that the Swartkrans was a "burial ground" for *Telanthropus* and not a living site, and that the absence of artefacts might be explained on these grounds. A similar explanation might account for the absence of *Telanthropus* from the Extension Site at Sterkfontein, for, as Oakley (1954) points out, primates do not as a rule die or leave the remains of their dead in the living place.

Further evidence will undoubtedly become available during the next few years to test the truth of the present hypothesis: that the Sterkfontein artefacts were the work of *Telanthropus* (Robinson, 1956). The present study of the Swartkrans metacarpals provides some support for this view. On purely morphological grounds the 4th meta-carpal fragment, provisionally attributed to *Telanthropus*, could well have belonged to a hand capable of tool-using if not tool-making. The 1st metacarpal on the other hand attributed to *Paranthropus*, while clearly pertaining to a hand capable of great

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* Artefacts are now known to exist at Swartkrans (Brain, 1958), but the manner of their discovery, from indiscriminate blasting for lime, makes it difficult to relate them to any particular time level.

power and prehensile ability, has features suggestive of a disproportionately short thumb. A hand with these proportions, while being perfectly capable of grasping and using a tool, might well have considerable difficulty in tool manufacture, which demands a degree of precision, in terms of finger and thumb opposition, that in turn depends on the relative lengths of these two digits. Nevertheless there is likely to have been a stage in the evolution of tool-making man when the hominids—not yet tool-makers—were as Bartholomew & Birdsell have recognised (1953): "continuously dependent on tools for survival". This need could have been fulfilled by extending the occasional habit of using and *discarding* suitably shaped stones to one of using and *preserving* them and later to one of *selecting and preserving* them. This latter activity supposes an ability to recognise the potential value of natural objects by past experience. These grades of tool-using would appear to form the essential cultural sequence from the occasional tool-users through the habitual tool-users to the fully fledged tool-makers. The robustness and the highly developed sesamoid formation of the 1st metacarpal of *Paranthropus* may well suggest that this aberrant hominid was an habitual tool-user.

ACKNOWLEDGMENTS

REFERENCES

BARTHOLOMEW, G. A. & BIRDSELL, J. B. 1953. Ecology and the Protohominids. *Amer. Anthrop.*, Lancaster, Pa, **55**: 481.

BEAN, R. B. 1931 Stature in Old Virginians. *Amer. J. phys. Anthrop.*, Philadelphia, **15**: 355–419.

BRAIN, C. K. 1958. The Transvaal Ape-man-bearing Cave Deposits. *Mem. Transvaal Mus.*, Pretoria, **11**.

BROOM, R. & ROBINSON, J. T. 1949. A new type of Fossil Man. *Nature, Lond.*, **164**: 322–323, fig.

—— 1949a. Thumb of the Swartkrans Ape-Man. *Nature, Lond.*, **164**: 841–842, fig.

—— 1950. Man contemporaneous with the Swartkrans Ape-Man. *Amer. J. phys. Anthrop.*, Philadelphia (n.s.) **8**: 151–156, 6 figs.

LE GROS CLARK, W. E. 1955. *The fossil evidence for human evolution.* x+180 pp.   Chicago.

MACALISTER, A. Unpublished data in possession of Anatomy School, Cambridge.

MIVART, ST. GEORGE. 1867. Contributions towards a more complete knowledge of the skeleton of the Primates, 1. The appendicular skeleton of *Simia*. *Trans. Zool. Soc. Lond.*, **7**: 175–225, pls. 35–43.

NAPIER, J. R. 1956. The prehensile movements of the human hand. *J. Bone Jt Surg.*, London, **38**, B, 4: 902–913.

OAKLEY, K. P. 1951. A definition of Man. *Sci. News*, London, **20**: 69–81.

—— 1954. Dating of the Australopithecinae of Africa. *Amer. J. phys. Anthrop.*, Philadelphia (n.s.), **12**: 9–27, pls. 1, 2.

—— 1957. Tools makyth man. *Antiquity*, Gloucester, **31**: 199–209.

ROBINSON, J. T. 1953. *Telanthropus* and its phylogenetic significance. *Amer. J. phys. Anthrop.*, Philadelphia (n.s.), **11**: 445–501, 14 figs.

—— 1954. The Genera and Species of the Australopithecinae. *Amer. J. phys. Anthrop.*, Philadelphia (n.s.) **12**: 181–200, 7 figs.

—— 1956. The dentition of the Australopithecinae. *Mem. Transvaal Mus.*, Pretoria, **9**. vii+179 pp.

ROBINSON, J. T. & MASON, R. J. 1957. Occurrence of stone artefacts with *Australopithecus* at Sterkfontein. *Nature, Lond.*, **180**: 521–524, 4 figs.

WELLS, L. H. A reconsideration of some mandibular profiles. *S. Afr. J. Sci.*, Cape Town, **54**: 55–58.

WILDER, H. H. 1926. *The pedigree of the human race.* xiv+368 pp., 1 pl.   London.

ABBREVIATIONS USED IN APPENDIX TABLE I

Sex   U = Sex unknown
Source   B.M. (N.H.) = British Museum (Natural History)
            R.C.S. = Royal College of Surgeons
            U. of W. = University of the Witwatersrand
Status   W.-S. = Wild-shot
            C. = Presumed captive
A.P.W. = Antero-posterior width in mid-shaft
T.W.   = Transverse width in mid-shaft
R.I.   = Index of robustness
R.C.   = Radius of curvature of head
F.   = Flat head
O–A   = Evidence of osteo-arthritis
n. r.   = not recorded

APPENDIX. TABLE I

DETAILS OF 1st METACARPAL BONES USED IN COMPARATIVE STUDY

Genus	Sex	Source	Status	Age classification	Length (mm.)	A.P.W. (mm.)	T.W. (mm.)	R.I.	R.C. (mm.)
Pan	U	B.M. (N.H.) 1861. 7.29.14 2K	C.	Adult	37·0	7·0	9·0	21·6	7
Pan	U	B.M. (N.H.) 2a	C.	Adult	35·0	6·5	9·0	22·2	F
Pan	U	B.M. (N.H.) 1948. 3.12.1	W.-S.	Adult	35·5	6·0	6·5	17·6	F
Pan	U	B.M. (N.H.) 1901. 8.9.10	C.	Adult	39·0	7·0	8·0	19·2	8
Pan	U	B.M. (N.H.) 1909. 8.9.84	W.-S.	Adult	39·0	6·0	7·5	17·3	10
Pan	F	B.M. (N.H.) 1951. 9.27.8	W.-S.	Adult	39·0	8·0	9·0	21·8	15
Pan	F	B.M. (N.H.) 1948. 5.7.2	W.-S.	Adult	38·0	5·5	7·0	16·5	20 (O–A)
Pan	U	B.M (N.H.) 1948. 10.25.2	W.-S.	Adult	41·0	7·0	8·5	16·5	10
Pan	U	B.M. (N.H.) 1948. 7.8.2	W.-S.	Adult	40·0	7·0	8·0	18·8	F (O–A)
Pan	U	B.M. (N.H.) 1922. 12.19.2	C.	Adult	48·5	9·0	10·0	19·6	8
Pan	U	B.M. (N.H.) 1881. 19.18.1	C.	Adult	41·0	7·0	10·5	18·9	F

Genus	Sex	Source	Status	Age classification	Length (mm.)	A.P.W. (mm.)	T.W. (mm.)	R.I.	R.C. (mm.)
Pan	U	B.M. (N.H.) 1883. 7.28.18	C.	Adult	41·0	6·5	7·5	17·1	4
Pan	U	B.M. (N.H.) 1924. 8.6.1	W.-S.	Young adult	46·0	8·5	7·0	16·9	8
Pongo	M	B.M. (N.H.) 3. C2	C.	Adult	52·5	7·5	10·0	16·67	10
Pongo	U	B M. (N. H.) 1948. 11.23.1	C.	Young adult	47·0	6·0	8·0	14·9	9
Pongo	U	B.M. (N.H.) 1948. 10.31	C.	Young adult	48·0	5·5	7.0	13·2	7
Pongo	U	B.M. (N.H.) 1948. 10.25.1	C.	Adult	46·0	6·5	7·5	15·2	8
Pongo	U	B.M. (N.H.) 1948. 7.6.3	C.	Adult	56·0	8·5	9·0	15·7	10
Pongo	U	B.M. (N.H.) 1948. 9.9.2	C.	Adult	45·5	6·5	10·0	18·2	10
Pongo	M	B.M. (N.H.) 3 L.	C.	Adult	52·5	7·5	9·5	16·2	15
Pongo	U	B.M. (N.H.) 1085	C.	Adult	56·5	8·5	11·0	17·3	9
Pongo	M	B.M. (N.H.) 1880. 4.10.1.3. 02	C.	Adult	53·5	7·5	9·0	15·4	8
Pongo	U	B.M. (N.H.) 1868. 4.16.2.3. R2	C.	Adult	50·0	9·0	10·0	19·0	7
Gorilla	U	B.M. (N.H.) 1948. 3.11.1	W.-S.	Adult	48·5	8·0	11·0	19·6	6
Gorilla	F	B.M. (N.H.) 1948. 3.3.1.2.	W.-S.	Adult	43·5	6·5	9·5	18·3	8
Gorilla	M	B.M. (N.H.) 1011h	W.-S.	Adult	48·0	8·5	12·5	21·4	10
Gorilla	U	B.M. (N.H.) 1916. 11.11.1	C.	Adult	45·0	7·0	9·5	18·3	9
Gorilla	F	B.M. (N.H.) 1948. 3.31.1	W.-S.	Adult	42·5	6·5	9·0	18·3	7
Gorilla	U	B.M. (N.H.) 1948. 4.1.1	W.-S.	Adult	48·0	9·0	11·0	20·9	8
Gorilla	U	B.M. (N.H.) 1948. 2.27.1	C.	Adult	49·0	9·0	11·5	21·0	8

Genus	Sex	Source	Status	Age classification	Length (mm.)	A.P.W. (mm.)	T.W. (mm.)	R.I.	R.C. (mm.)
Gorilla	M	B.M. (N.H.) 1948. 3.3.2	W.-S.	Adult	55·5	11·0	11·0	19·8	9
Gorilla	U	B.M. (N.H.) 1011c	W.-S.	Adult	39·0	6·5	9·5	20·6	8
Gorilla	F	B.M. (N.H.) 1949. 12.20.2	W.-S.	Adult	42·0	9·0	9·5	23·2	8
Gorilla	U	B.M. (N.H.) 9.27.11	C.	Adult	48·0	10·0	15·0	26·1	10
Gorilla	F	B.M. (N.H.) 12.1.1	C.	Adult	38·5	6·0	9·0	19·5	5
Gorilla	U	B.M. (N.H.) 1949. 12.30.2	W.-S.	Adult	46·0	10·0	11·5	23·4	9
Gorilla	U	B.M. (N.H.) 12.1.5. 1011o	W.-S.	Adult	39·0	6·0	9·0	19·3	8
Gorilla	M	B.M. (N.H.) 1864 12.1.13.	—	Adult	53·5	9·5	12·0	20·1	10
Gorilla	U	B.M. (N.H.) 1948. 436	C.	Adult	51·5	8·5	12.5	20·4	10
Homo (Bushman)	F	R.C.S. 1300. No. 4 (18)	—	Adult	37·0	7·5	10·0	23·7	25
Homo (Bushman)	F	R.C.S. 1300. No. 14 (18)	—	Adult	39·0	7·5	9·5	21·8	10
Homo (Bushman)	F	R.C.S. 1300. No. 15	—	Adult	42·5	7·5	9·5	15·1	15
Homo (Bushman)	F	R.C.S. 1300. No. 17 (8)	—	Adult	42·0	6·5	10·0	19·7	35
Homo (Bushman)	F	R.C.S. 1300. No. 11	—	Adult	41·0	7·5	11·5	23·2	10
Homo (Bushman)	F	R.C.S. 1300. No. 18	—	Adult	36·0	6·5	9·0	21·5	8
Homo (Bushman)	F	R.C.S. 1302	—	Adult	34·5	6·0	9·5	22·3	20
Homo (Bushman)	F	R.C.S. 1300. No. 16	—	Adult	41·0	8·0	11·5	23·8	25
Homo (Bushman)	M	B.M. (N.H.) 47. 1921.12.17.1	—	Adult	39·0	6·5	9·5	20·6	10
Homo (Bushman)	F	Anat. Mus. Cambridge	—	Adult	42·0	n.r.	n.r.	n.r.	n.r.

Genus	Sex	Source	Status	Age classiffcation	Length (mm.)	A.P.W. (mm.)	T.W. (mm.)	R.I.	R.C. (mm.)
Homo (Bushman)	M	Anat. Mus. Cambridge	—	Adult	36·0	n.r.	n.r.	n.r.	n.r.
Homo (Bushman)	U	U. of the W. A319	—	Adult	48·9	8·8	12·3	21·5	n.r.
Homo (Bushman)	U	U. of the W. A26	—	Adult	46·2	7·3	9·9	18·6	n.r.
Homo (Bushman)	U	U. of the W. A379	—	Adult	36·9	8·0	10·8	25·5	n.r.
Homo (Bushman)	M	U. of the W. A327	—	Adult	41·4	7·4	10·9	22·1	n.r.
Homo (Bushman)	U	U. of the W. A123	—	Adult	36·4	6·9	9·2	22·1	n.r.
Homo (Bushman)	U	U. of the W. A390	—	Adult	47·8	9·4	13·3	23·7	n.r.
Homo (Bushman)	F	U. of the W. A272	—	Adult	37·7	7·8	8·7	21·9	n.r.
Homo (Bushman)	U	U. of the W. A240	—	Adult	44·8	8·4	10·9	21·3	n.r.

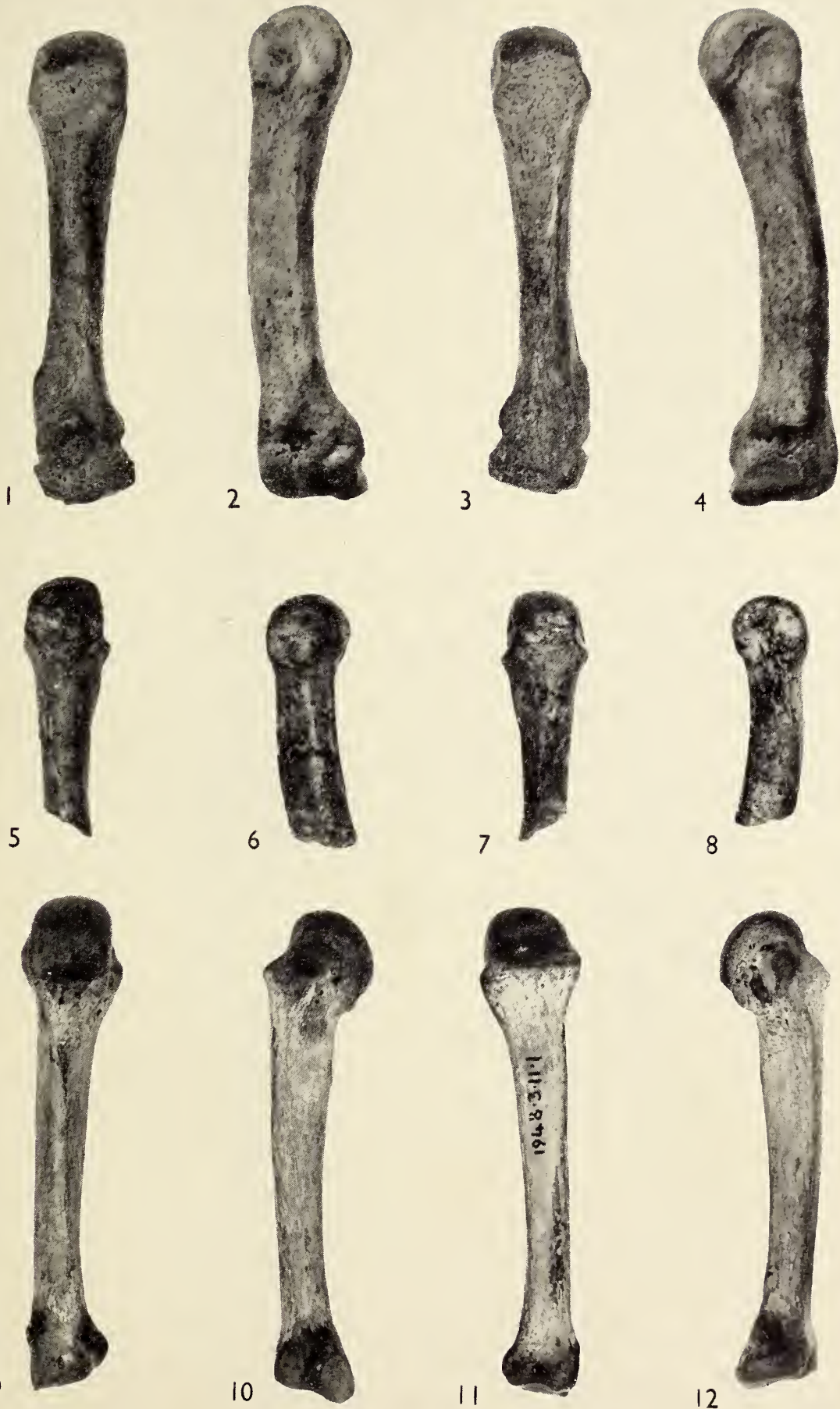PLATE 1

EXPLANATION OF PLATE 1

FIGS. 1–4.   Four views of the 4th metacarpal (L) of *Homo*.   × 1½.

FIGS. 5–8.   Four views of the left 4th metacarpal fragment (S K.85) of *Telanthropus*.   × 1¼.

FIGS. 9–12. Four views of the 4th metacarpal (L) of *Gorilla*.   × 1.   B.M. (N.H.) 1948.3.11.1.

Brit. Mus. (Nat. Hist.)
Fossil Mammals of Africa, 17

PLATE 1

4th METACARPALS (L)

PLATE 2

Brit. Mus. (Nat. Hist.)
Fossil Mammals of Africa, 17

PLATE 2

1st METACARPALS (L)